Common trends in German Bight benthic macrofaunal communities: Assessing temporal variability and the relative importance of environmental variables

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ABSTRACT

We examined long-term variability in the abundance of German Bight soft bottom macro-zoobenthos together with major environmental factors (sea surface temperature, winter NAO index, salinity, phosphate, nitrate and silicate) using one of the most comprehensive ecological long-term data sets in the North Sea (1981–2011). Two techniques, Min/Max Autocorrelation Factor Analysis (MAFA) and Dynamic Factor Analysis (DFA) were used to identify underlying common trends in the macrofaunal time series and the relationships between this series and environmental variables. These methods are particularly suitable for relatively short (>15–25 years), non-stationary multivariate data series. Both MAFA and DFA identify a common trend in German Bight macrofaunal abundance i.e. a slight decrease (1981–mid-1990s) followed by a sharp trough in the late 1990s. Subsequently, scores increased again towards 2011. Our analysis indicates that winter temperature and North Atlantic Oscillation were the predominant environmental drivers of temporal variation in German Bight macrofaunal abundance. The techniques applied here are suitable tools to describe temporal fluctuations in complex and noisy multiple time series data and can detect distinct shifts and trends within such time series.

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1. Introduction

Benthic macrofauna plays an important role in the structure and functioning of marine ecosystems (Brey, 2012; Oug et al., 2012). Benthic species are consumed by fish, birds and mammals, thereby providing food for higher trophic levels (Iken et al., 2010). Macrobenthos is also important in nutrient and organic matter cycling and provides an important link between the benthic and pelagic compartment of marine ecosystems (Grall and Chauvaud, 2002; Hill et al., 2011). These functions as well as the relatively stationary habit of many benthic organisms make them sensitive bio-indicators of environmental change (Tomiyama et al., 2008). Benthic communities may fluctuate over time because of characteristics of the species' life cycles and/or in response to environmental variability (Convey, 1996; Sibly and Calow, 1989). In this context, assessing temporal patterns of benthic community development and their underlying drivers is critical for understanding the ecology of diverse marine ecosystems (Robinson and Sandgren, 1983; Zajac et al., 2013). In fact, understanding patterns of change in benthic fauna through

the monitoring of communities (e.g., community structure and composition, species richness) might allow for separating effects of climate variability and anthropogenic disturbance on diversity and the functioning of the marine benthic ecosystem (Munari, 2011).

There are a number of multivariate analysis techniques (e.g. redundancy analysis and canonical correspondence analysis) available to analyze interactions between different variables in time. Here, we prefer Min/Max Autocorrelation Factor Analysis (MAFA) and Dynamic Factor Analysis (DFA), since these two approaches allow estimation of common patterns and interactions in various time series and also inspection on the effect of explanatory time-dependent parameters (Ritter and Muñoz-Carpena, 2006; Zuur et al., 2007). MAFA and DFA are particularly suitable for relatively short (>15–25 years), non-stationary multivariate time series data. MAFA takes the temporal autocorrelation structure into account and extracts significant common trends from the data (Zuur et al., 2007). It also quantifies the canonical correlation between temporal trends and macrofaunal abundance time series (Nye et al., 2010). DFA is used to identify underlying common trends among multivariate time series while taking the effects of explanatory variables into account (Kuo and Lin, 2010; Zuur and Pierce, 2004). Here, we focus on a 30 year (1981–2011) time series of benthic macrofaunal abundance and environmental variables in the German Bight. The specific objectives of

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our study were (i) to analyze this data set for common temporal patterns and (ii) to identify the environmental factors affecting these temporal patterns.

2. Material and methods

2.1. Response variables

The database of this study consists of macro-zoobenthos samples collected at four stations in the German Bight in spring (i.e. prior to the main seasonal recruitment period) 1981 to 2011 (Fig. 1). The stations represent the typical bottom communities in this region, i.e. the *Nucula nitidosa*-, *Tellina fabula*- and *Amphiura filiformis*-associations (Salzwedel et al., 1985; Schröder, 2003). Samples were collected using 0.1 m^2 Van Veen grabs, sieved over 0.5 mm mesh and fixed in 4% buffered formalin. Macro-zoobenthic organisms were identified to species level as far as possible, counted and weighed (wet weight). The data used in this study are total taxa abundance per square meter and per sampling date and station. A total of 152 taxa were encountered during the entire sampling series. In order to identify those taxa which were most representative for the overall trend in community composition, data of all four stations were pooled and a Biota-Environment Stepwise Analysis (BVSTEP) (Clarke and Warwick, 1998) was applied to the 31 sampling dates × 152 taxa abundance matrix.

BVSTEP involves a stepwise 'forward selection and backward elimination' algorithm allowed determination of the small subset of species whose similarity matrix best matched that of the full data at $\rho > 0.95$ level of Spearman's rank correlation (Clarke and Gorley, 2006). This small subset of variables encapsulated most of the explanatory power of the original data and thus, was most representative for the overall trend in community composition. Abundance data were fourth-root transformed prior to analysis to reduce the influence of very abundant taxa on the relationship between samples (Clarke and Warwick, 1998). This analysis was performed using the PRIMER v6 (Plymouth Routines in Multivariate Ecological Research) (Clarke and Gorley, 2006).

2.2. Explanatory variables

Several environmental parameters were tested for their effects on the long-term trends of macrofaunal abundance: mean sea surface temperature (SST) during winter (Dec.–Mar.; SSTw) and summer of the preceding year (Jul.–Sep.; SSTs), mean salinity and dissolved inorganic nutrient concentrations (phosphate, nitrate and silicate) were derived from the Helgoland Roads long-term data set (Wiltshire et al., 2010); daily measurements at station "Kabeltonne" (54°11′3″ N, 7°54′0″ E) between the two Helgoland islands since 1962. The North Atlantic Oscillation annual (NAOI) and winter indices (NAOWI) (Dec.–Mar) were obtained from Climate Analysis Section, NCAR, Boulder, USA (http://www.cgd.ucar.edu/cas/jhurrell/indices.html). The variables were lagged up to two years in order to explore possible indirect or delayed effects of environmental pressures on benthic macrofauna.

2.3. Data exploration

Each macrofaunal and environmental parameter time series was standardized to mean = 0 and standard deviation = 1 to simplify the interpretation of the estimated regression parameters (Zuur et al., 2007). We applied variance inflation factor (VIF) analysis to identify and to eliminate the variables that are collinear (Zuur et al., 2007) as multi-collinearity may introduce bias into the analysis (Zuur et al., 2007). VIF is a scaled version of the multiple correlation coefficients between variable δ and the rest of the independent variables expressed as:

$$VIF_\delta = 1/\left(1 - R_\delta^2\right) \qquad (1)$$

where R^2_δ is the multiple correlation coefficient (Graybill and Iyer, 1994). A threshold VIF of 5 was set as the maximum, meaning that a value >5 indicates potential multi-collinearity (Ritter and Muñoz-Carpena, 2006).
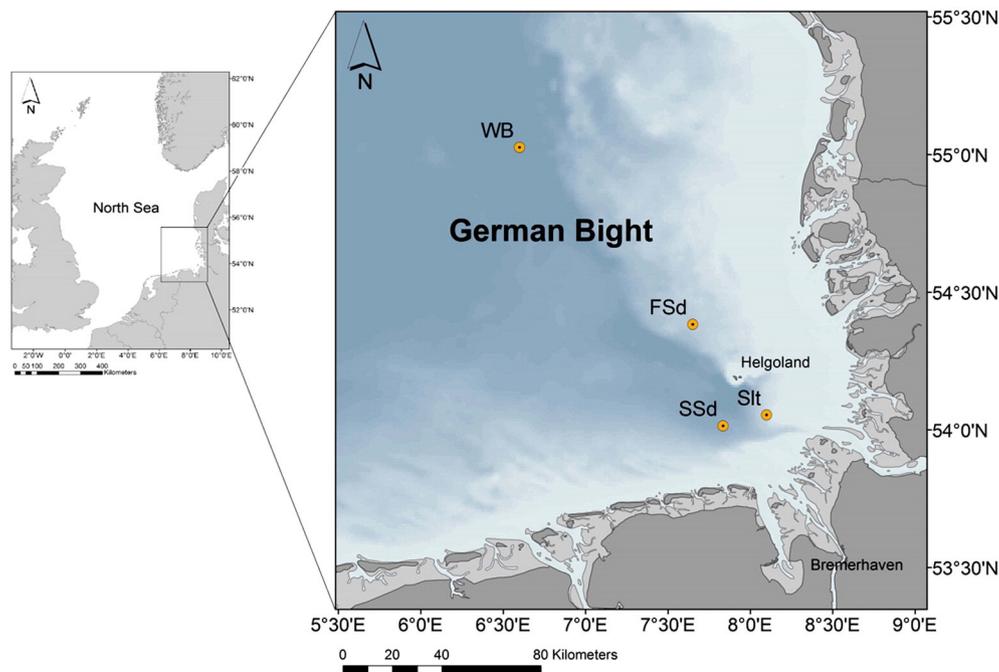

Fig. 1. Location of the four long-term monitoring stations for macro-zoobenthos in the German Bight, North Sea.

2.4. Min/max autocorrelation factor analysis (MAFA)

MAFA is a type of principal component analysis (PCA) for short time series, first developed to separate signals from noise in multivariate imagery observation (Switzer and Green, 1984). Later, MAFA was adapted to analyze and extract patterns from multiple time series (Shapiro and Switzer, 1989; Woillez et al., 2009). MAFA decomposes the set of initial variables into a series of axes (the MAFs), in which autocorrelation (with time lag 1) decreases from the first to the last axis (Woillez et al., 2009). The underlying assumption is that a trend is associated with high autocorrelation with time lag 1 (Ligas et al., 2010). Therefore, the first MAFA axis represents the trend or extracts the part that is the most continuous in time (Woillez et al., 2009). Canonical correlation between macrofaunal time series and MAFA axes was applied to identify significant relationships between the variables and the trends (Zuur et al., 2007).

2.5. Dynamic factor analysis (DFA)

DFA is a multivariate time-series analysis technique to estimate common trends, to study the interactions between response variables and to determine the effects of explanatory variables in a time series data set (Zuur and Pierce, 2004; Zuur et al., 2003a). The underlying DFA model is given by (Zuur and Pierce, 2004):

$$\text{N time series} = \text{constant} + \text{linear combination of M common trends} + \text{explanatory variables} + \text{noise} \tag{2}$$

DFA describes a set of N observed time series and aims to keep M as small as possible while still producing an optimal model fit (Kisekka et al., 2013). Including explanatory variables partly reduces unexplained variability in the observed time series (Kisekka et al., 2013; Zuur et al., 2003b).

Eq. (2) translates into Eq. (3) (Kisekka et al., 2013; Kuo et al., 2011; Ritter and Muñoz-Carpena, 2006; Zuur and Pierce, 2004; Zuur et al., 2007):

$$ZB_n(t) = C_n + \sum_{m=1}^{M}\gamma_{m,n}\alpha_m(t) + \sum_{k=1}^{K}\beta_{k,n}e_k(t) + \varepsilon_n(t) \tag{3}$$

with $\alpha_m(t)$ being defined as:

$$\alpha_m(t) = \alpha_m(t-1) + \rho_m(t) \tag{4}$$

where $ZBn(t)$ is the value of the nth time series (i.e. the abundance of 11 taxa) at time t (with $1 \leq n \leq N$). C_n is a constant level parameter as in linear regression model which increases or decreases the linear combination of common trends (Kuo and Lin, 2010). If the time series are standardized, the constant parameters are 0 (Zuur and Pierce, 2004).

$\sum_{m=1}^{M}\gamma_{m,n}\alpha_m(t)$ is a linear combination of common trends, in which $\alpha_m(t)$ is the mth unknown common trend (with $1 \leq m \leq M$) at time t and $\gamma_{m,n}$ is the factor loading that indicates the importance of each of the common trends to each response variable (Kisekka et al., 2013; Kuo et al., 2011). Factor loading (A cut-off point of 0.15) was applied to test which common trends are related to the macrofaunal time series (Ligas et al., 2010). $e_k(t)$ is a vector containing explanatory variables, and $\beta_{k,n}$ stands for the regression coefficient for the explanatory variables which indicates the relative importance of the explanatory variables to each time series (Zuur and Pierce, 2004). Whether the environmental variables are significantly related to taxa abundance was assessed by using the magnitude of the $\beta_{k,n}$ coefficients and their associated t-value (t-values larger than 2 in absolute value indicate a strong significant correlation); $\varepsilon_n(t)$ and $\rho_m(t)$ are assumed to be independent and homogeneous for each time series. We tested several DFA models by choosing different combinations of numbers of common trends, explanatory variables at lag = 0, 1 and 2, and symmetric non-diagonal

or diagonal covariance matrix. A higher number of common trends will introduce unexplained information that cannot be interpreted easily in the DFA model. Therefore, DFA should be handled with a model that produces a reasonable fit with the smallest number of common trends (Zuur et al., 2003b). The goodness-of-fit of the model can be assessed by visual inspection, the Nash–Sutcliffe coefficient of efficiency (NSE) (Nash and Sutcliffe, 1970) and the Akaike's Information Criterion (AIC; (Akaike, 1974). NSE provides an estimate of how well the time series of each taxon is represented by the best fitting DFA model, while the AIC is a statistical criterion for model selection with the best model having the lowest AIC (Zuur et al., 2007). Data exploration and analysis were carried out using the software package Brodgar 2.7.2 (http://www. brodgar.com).

3. Results

The BVSTEP procedure identified a subset of 25 taxa (Table 1), that explained 95% of the multivariate ordination pattern in the complete data matrix (BVSTEP, Spearman's ρ > 0.950 with 0.1% significance level). However, we detected high multi-collinearity between the 25 taxa and, hence, reduced the response variable data set to 11 taxa which we considered to be the best trade-off between minimum cross-correlation and maximum explanatory power (Table 1). The time series of these eleven taxa were summed up to the macrofaunal time series used for further analysis. Multiple co-linearity between environmental variables led to the exclusion of SSTs (lag = 1,2), SSTw (lag = 1,2), salinity (lag1, 2), nitrate (lag = 2) and NAOI (lag = 0, 1 and 2) from subsequent analysis. Cross correlation of the remaining environmental variables was ≤0.31.

3.1. Temporal development

The standardized macrofaunal abundance series are characterized by interannual fluctuations (Fig. 2). However, a similar variation pattern for different taxa can be detected as indicated by the smoothing curves. An overall increasing trend in abundance was apparent for *Abra* spp.,

Table 1
Representative taxa, explained 95% of the multivariate ordination pattern in the complete data matrix. Codes indicate the 11 taxa selected for time series analysis.

| Taxon	Code
Abra spp.	ABR
Amphiuridae	AMP
Bathyporeia spp.	BAT
Callianassa spp.	CAL
Capitellidae	–
Cylichna cylindracea	–
Diastylis spp.	–
Echinocardium cordatum	ECC
Glycera spp.	–
Lanice conchilega	–
Lumbrineris spp.	–
Magelona spp.	–
Nucula spp.	NUC
Ophiura spp.	OPH
Owenia fusiformis	–
Pectinaria spp.	–
Perioculodes longimanus	–
Pholoe baltica	–
Poecilochaetus serpens	–
Scoloplos armiger	–
Spio filicornis	SPF
Spiophanes bombyx	SPB
Spisula spp.	SPI
Sthenelais spp.	–
Thyasira flexuosa	THF
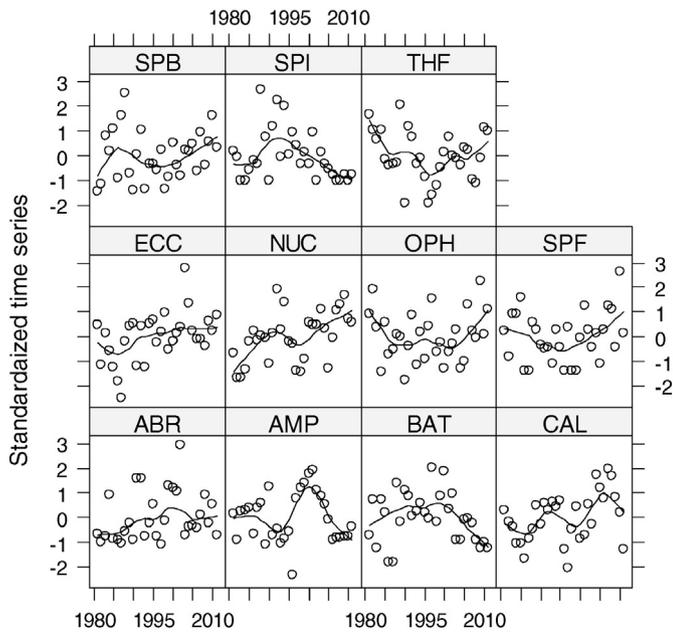
Fig. 2. Standardized benthic macrofaunal abundance time-series in the German Bight. The open circles and lines denote the observed abundance and overall smoothed curve, respectively (see Table 1 for species codes).

Echinocardium cordatum, *Nucula* spp. and *Callianassa* spp. *Ophiura* spp. and *Thyasira flexuosa* displayed a decrease in abundance within the first half of the series, followed by an increase towards the end. *Spisula* spp. and *Bathyporeia* spp. displayed the opposite response with an increase in abundance during the first half of the series and a decrease thereafter. The trend for the Amphiuridae showed a dip in mid-1990s and a high peak around 2001. *Spiophanes bombyx* increased in abundance until 1990 and slightly decreased thereafter. The abundance of *Spio filicornis* slightly decreased until mid-1990s and remained relatively constant until the end of the series.

Similar to the abundance time series, all selected environmental variables exhibited wide fluctuations (Fig. 3 and Appendix A). There

was an overall increasing trend in SSTw, SSTs and salinity, while nitrate, phosphate and silicate showed an overall decreasing trend (except for 1981–1987). There was no overall temporal trend in NAOI and NAOWI and both variables fluctuated irregularly throughout the entire time series.

3.2. MAFA

The main trend (MAFA axis) that was derived from the 11 macrofaunal time series is shown in Fig. 4.a (autocorrelation of 0.85 at p < 0.005). The MAFA axis showed a slight decrease in abundance until the mid-1990s followed by a sharp trough in the late 1990s. Canonical correlations between MAFA axis and taxa (Fig. 4.b) indicate that three taxa (*Callianassa* spp., *S. filicornis*, and *T. flexuosa*) correlated significantly positively (p < 0.05) with the axis, whereas *Spisula* spp. correlated negatively (p < 0.05).

3.3. DFA

Among the various DFA models tested, the model consisting of one common trend, some environmental variables (SSTw, SSTs, NAOWI, NO3, PO4, SiO2) and a symmetric non-diagonal matrix fitted the data best (Table 2). The inclusion of time lagged explanatory variables in the DFA model reduced the AIC of DFM and improved the description of the temporal development of benthic abundance in the German Bight. The common trend shows two distinct declines from 1981 to 1985 and 1993 to 1999. Each decline is followed by an increase (Fig. 5.a). Factor loadings illustrate the relation between common trends and time series (Fig. 5.b). The common trend was positively (factor loading values were higher than the selected cut-off level of 0.10) correlated with *Callianassa* spp., *Ophiura* spp., *S. filicornis* and *T. flexuosa* and negatively correlated with *Abra* spp., Amphiuridae, *Bathyporeia* spp. and *Spisula* spp. The regression coefficients for the explanatory variables (Table 3) indicate that ten taxa had a significant relationship with the environmental variables (t > 2). The t-values indicate that SSTw was significantly related to the largest number of abundance series: *Abra* spp., Amphiuridae, *Callianassa* spp., *E. cordatum*, *S. filicornis*, *Spisula* spp. and *T. flexuosa*, whereas nitrate was significantly related to only one taxon (*T. flexuosa*). The model performed well (NSE > 0.50) for most of the
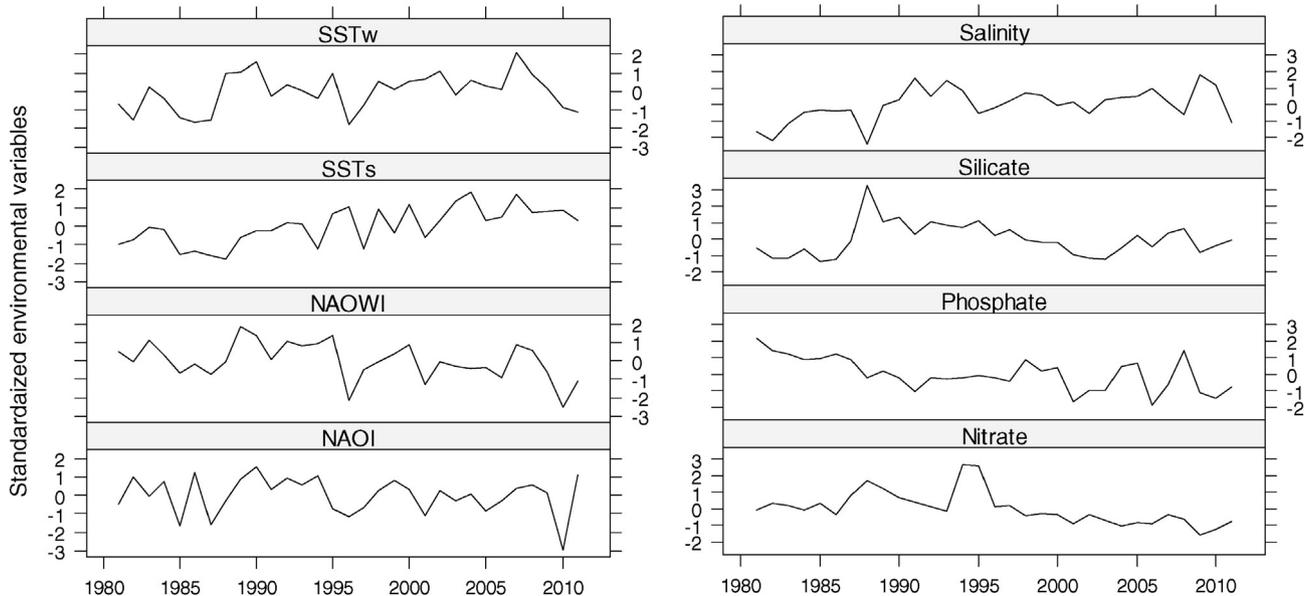

Fig. 3. Standardized time series of environmental variables used in DFA model.
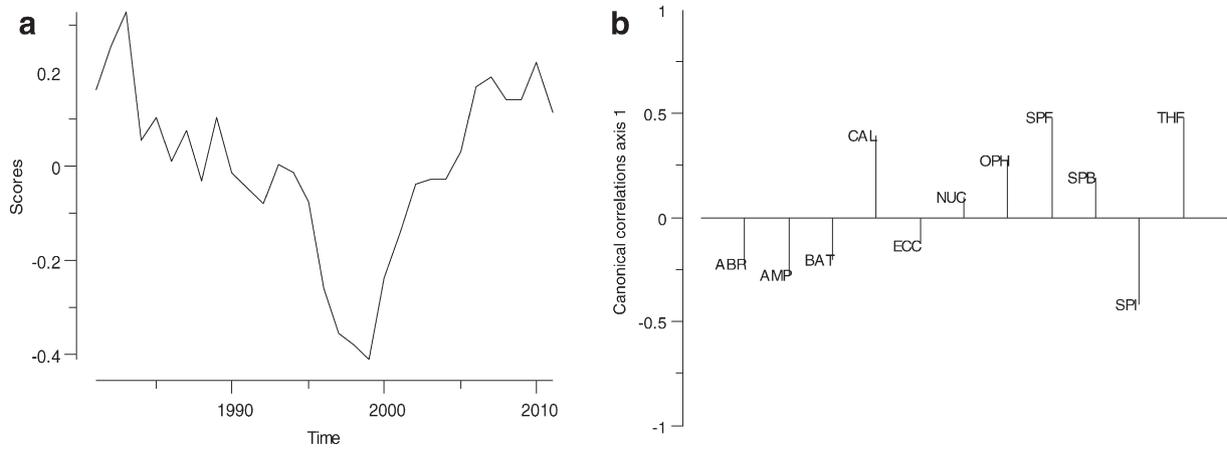
Fig. 4. (a) The main trend identified by MAFA in the abundance of 11 taxa in the German Bight. (b) Canonical correlations between taxa and MAFA axis for the main trend in macrofaunal abundance in the German Bight. Significance level for correlation = 0.36.

taxa abundance time series (except for *Bathyporeia* spp.), indicating that most time series fitted well in the estimated model.

4. Discussion

Biological time series produce valuable datasets that can identify ecological patterns and how they link to climate variability and to anthropogenic stressors (PISCO, 2009). Accordingly, time series have been used for management and policy applications, for example, in the context of eutrophication (Rachor and Schröder, 2003), impacts of offshore wind energy facilities (Lindeboom et al., 2011) and management of endangered species (Beissinger and Westphal, 1998). Our analysis revealed substantial variation in macrozoobenthos community composition in the German Bight at decadal and sub-decadal scales. The optimal DFA model indicated that SSTw and NAOWI (lag = 1) play a distinct role in controlling the temporal variation of the benthic macrofaunal assemblages. Our discussion addresses (i): Which environmental variables drive the development of benthic communities in the North Sea? (ii) Which taxa contribute most to the temporal development of macrofaunal communities?

4.1. Common trends

Both MAFA and DFA techniques generally identified similar major temporal development of the benthos during the time series. A slight decrease in total macrofaunal abundance until the mid-1990s was followed by a sharp drop in the late 1990s (Figs. 4 and 5). Subsequently,

the trend increased until the end of the time series in 2011. In combination the two analytical procedures were able to reveal the dominant temporal trends in the benthic macrofauna of the German Bight. In the 1980s southern North Sea benthos was strongly shaped by low SST (e.g., 1984–1987) resulting in reduced abundances of warm-temperate species (e.g. *S. filicornis*) and elevated abundances of cold-temperate species (e.g. *Spisula* spp.) (Kröncke et al., 1998; Wieking and Kröncke, 2003). A sharp drop in benthos abundances in the late 1990s coincided with the exceptionally cold winter in 1995/1996 (Schröder, 2003), the most notable event in the hydro-climate of the German Bight at that time (Reiss et al., 2006). A similar overall decreasing trend and a big drop in the Wadden Sea (southern North Sea) benthic macrofaunal abundance have been reported for the periods 1983–1988 and mid-1990s, respectively (Dippner and Kröncke, 2003). Our findings correspond to the observations of Neumann et al. (2009), who report an increase in epifaunal abundance and species diversity in the southern North Sea between 2003 and 2008.

4.2. Relative contribution of explanatory variables

DFA model regression coefficients indicated that SSTw was the dominant environmental factor determining the temporal dynamics of the benthic macrofauna (Table 3). This result indicates that similar to other studies (Beukema, 1992; Wadden Sea, Dippner and Ikauniece, 2001; Eastern Baltic Sea, Kröncke et al., 1998; German Bight and Rumohr, 1986; Western Baltic Sea) the inter-annual variability in macrozoobenthos abundance during spring in the German Bight is influenced by the climate variability during the preceding winter. The importance of temperature in structuring the marine benthic macrofauna has repeatedly been reported in previous studies (Neumann and Kröncke, 2011; Neumann et al., 2009; Zuur et al., 2003b). Fluctuations in temperature can be expected to affect benthic organisms both directly and indirectly (Brodersen et al., 2011). Temperature directly influences key reproductive processes, such as gametogenesis and spawning, with crucial effects on recruitment (Occhipinti-Ambrogi, 2007). Indirect effects on organisms include alteration of trophic interactions, population dynamics, and competition (Brodersen et al., 2011). Extreme changes in temperature (e.g. severe winters) in the North Sea, may dramatically affect benthic species through direct mortality. This could translate into decreasing species richness, abundance and biomass (Neumann et al., 2009; Reiss et al., 2006; Schröder, 2003; Wieking and Kröncke, 2003). A variety of taxa were found to respond to temperature in terms of abundance fluctuations (i.e. *Abra* spp., Amphiuridae, *Callianassa* spp., *E. cordatum*, *S. filicornis*, *Spisula* spp. and *T. flexuosa*, see Table 3), and various previous studies have

Table 2
Selection of dynamic factor models (DFMs) with one and two common trends. The optimal DFA model based on Akaike's information criterion (AIC) is in bold.

| Model	Akaike's information criterion (AIC)			
	Symmetric non-diagonal		Diagonal matrix	
Explanatory variables	1	2	1	2
None	982.97	998.92	998.98	1002.71
SSTw, SSTs, Salinity, NAOWI, NO₃, PO₄,SiO₂	971.14	976.31	1022.43	1024.91
SSTw, SSTs, NAOWI, NO₃, SiO₂, PO₄	964.27	970.11	1015.13	1009.01
NAOWI(L = 1, 2), NO₃ (L = 1), PO₄ (L = 1, 2), SiO₂ (L = 1, 2)	942.13	944.82	987.47	976.63
SSTw, SSTs, NAOWI (L = 0–2), NO₃ (L = 0, 1), PO₄ (L = 0–2), SiO₂ (L = 0–2)	**866.03**	872.91	970.67	989.67
NAOWI (L = 0–2)	995.42	995.03	1008.01	1007.45
SSTw, SSTs	958.16	960.45	981.93	983.14
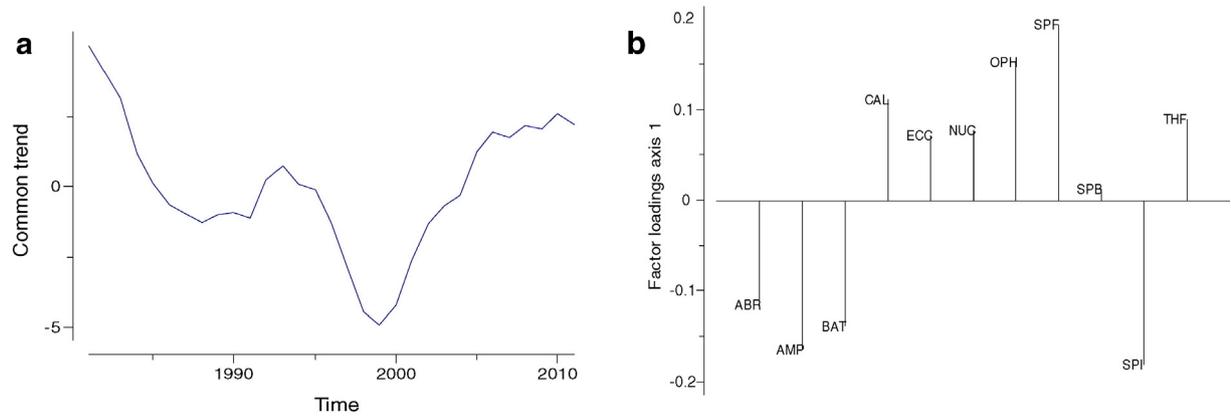
Fig. 5. (a) Common trend and (b) corresponding associated factor loading for macrofaunal time series obtained by means of DFA containing one common trend and several explanatory variables based on a symmetric non-diagonal matrix (see Table 1 for species codes).

demonstrated the temperature sensitivity of these species (Carpenter et al., 1997; Dekker and Beukema, 1999; Reiss et al., 2006). For instance, the bivalves *Abra* spp. displayed significant changes in abundance related to mild (high abundance) and severe (low abundance) winters (Birchenough and Bremner, 2010). The conspicuous implications of extreme temperature events probably explain why the continuous increase in SST in the North Sea over the past five decades (Wiltshire et al., 2008) has not resulted in an equally continuous change in macrozoobenthos abundance but causes fluctuations at a decadal and sub-decadal temporal scale. The sensitivity to temperature variations differs within and among species. Species vary ontogenetically in their susceptibility to habitat stress (Harley et al., 2006). Planktonic larvae are principally susceptible to thermal effects and young benthic stages are often more sensitive to environmental stress than adults (Harley et al., 2006; Pechenik et al., 1996). The specific temporal fluctuations in species abundances in response to environmental variations result in the observed overall fluctuation in macrozoobenthos community composition. Accordingly, the prediction of the future state of macrozoobenthos communities in the German Bight is rather complex, and requires knowledge of the probability of occurrence of certain climate anomalies in the near and longer term future, and of the effects of this variability on function and interactions of different species and on food webs (Livingston et al., 2005).

In addition to temperature, some lagged and un-lagged environmental factors also affected temporal variability (Table 3). Note that considering time lag effects in the dynamic factor model, the AIC of DFMs was improved distinctly, as shown in the Table 2. Apparently, some environmental factors cause immediate responses of benthic populations (mostly through mortality) while other factors affect specific

life history traits (e.g. reproduction and development) thereby inducing a lagging population response (Gröger and Rumohr, 2006). Interactions between species (e.g., certain trophic levels) may also produce time lags. This can be either prey or predator organisms or competition (Gröger and Rumohr, 2006). This is presumably not the case for macrozoobenthos of the German Bight since the biological interactions such as competition for space and food are of minor importance for variation at the community levels.

NAOWI (lag = 1) is the second most important factor after temperature. Time lags in the response of benthic communities to climatic variability associated with NAO are widespread in marine environments (Ottersen et al., 2001). The effects of climate variability on marine organisms involve three principal categories: direct effects, indirect effects and integrated effects under consideration of lagged and un-lagged response (Dippner, 2006). The direct effects of NAO are mechanisms that involve an un-lagged direct ecological response to the environmental circumstances synchronized with the NAO, (e.g., the effect of the NAO on the abundance of marine polychaetes via the winter temperature effects on a predatory-prey interaction; Beukema et al., 2000). Indirect effects either include several biological or physical mediators between NAO and the ecological trait and/or have no direct impact on the biology of the population (e.g., indirect effects of NAO on the abundance of macrofaunal community through pelagic primary production; Tunberg and Nelson, 1998; Kröncke et al., 1998). Integrated effects involve simple ecological responses that occur during and after a NAO extreme (Dippner, 2006). This is the case when a community has to be repeatedly affected by a particular environmental situation before the ecological change can be perceived or when the environmental phenomenon affecting the population is itself modulated over a number

Table 3
Factor loadings ($\gamma_{m,n}$) corresponding to the common trend and regression coefficients for the explanatory variables. The bold characters represent the environmental variables which were statistically significant (t > 2). Species codes are given in Table 1.

Time series	$\gamma_{1,n}$	Regression coefficients											
		β_{SSTw}	β_{SSTs}	β_{NAOWI}	$\beta_{NAOWI-L1}$	$\beta_{NAOWI-L2}$	$\beta_{Nitrate}$	$\beta_{Nitrate-L1}$	$\beta_{Phosphate}$	$\beta_{Phosphate-L1}$	$\beta_{Phosphate-L2}$	$\beta_{Silicate}$	$\beta_{Silicate-L1}$	$\beta_{Silicate-L2}$
ABR	−0.11	**0.59**	0.04	0.01	**0.37**	**0.34**	−0.10	−0.40	0.09	−0.40	0.21	−0.06	0.13	−0.10
AMP	−0.16	**0.62**	**−0.47**	0.04	−0.09	−0.20	0.00	−0.22	−0.05	0.13	−0.11	−0.25	**−0.50**	0.18
BAT	−0.01	0.40	0.34	−0.22	0.00	0.31	0.31	**−0.46**	0.11	0.25	0.06	0.09	0.37	0.09
CAL	0.11	**0.36**	**0.37**	−0.04	**0.55**	−0.04	0.38	**−0.50**	0.05	−0.06	0.01	−0.02	0.24	−0.30
ECC	0.09	**0.54**	**0.39**	−0.28	**−0.44**	−0.12	**0.50**	0.12	−0.07	0.20	**−0.40**	0.07	0.24
NUC	0.07	0.27	−0.09	0.32	**0.38**	0.28	−0.10	0.25	**−0.40**	**−0.57**	−0.13	0.18	0.06	**−0.39**
OPH	0.16	−0.11	0.22	−0.14	**−0.70**	0.21	0.31	−0.09	−0.12	**0.52**	−0.16	−0.25	**0.49**	0.10
SPF	0.12	**0.53**	−0.11	−0.02	0.25	**0.38**	0.17	0.31	−0.04	−0.21	0.13	−0.07	0.17	−0.20
SPB	0.01	−0.09	0.32	−0.02	−0.03	**0.49**	0.03	−0.20	−0.14	0.02	**0.27**	**0.64**	−0.29	**−0.50**
SPI	−0.18	**−0.54**	0.12	0.18	−0.16	0.12	0.25	−0.16	−0.28	**0.39**	**−0.32**	0.23	**0.33**	**−0.35**
THF	0.01	**−0.42**	−0.07	**0.65**	0.18	0.04	−0.13	**−0.43**	**−0.40**	−0.14	**0.38**	−0.06	**0.39**	**−0.57**

of years (e.g., reduction of the volume of Norwegian Sea Deep Water (NSDW) and its effect of the abundance of *C. finmarchicus* in the North Sea; Ottersen et al., 2001; Visbeck et al., 2003).

NAO has long been considered as a very good predictor in forecasting benthic time series (Kröncke, 2011). However, after the regime shift in 2000/2001 the correlation between NAO and macrofauna biomass and abundance diminished, perhaps reflecting the disappearance of autocorrelation and thus predictability (Dippner et al., 2010; Junker et al., 2012; Kröncke et al., 2013). Presumably, this may be the reason that the DFM exhibited the highest AIC when we consider NAOWI as the only explanatory variable. Apparently, adding other explanatory variables to the model improves overall model fit. After 2000, the time series of the NAO behaved in a chaotic manner (Dippner et al., 2014). During this period, when the southern North Sea was mainly forced by SST anomalies and meridional winds, the total biomass and abundance as well as the abundance of dominant taxonomic groups (except for crustacean) increased distinctly (Dippner et al., 2014; Kröncke et al., 2013).

The optimal DFA model indicates that dissolved inorganic nutrients play a significant role in the long-term dynamics of the benthic macrofauna. Increased nutrient concentration in marine waters increases surface primary production and hence the food supply to macrofauna populations (Josefson, 1990). Therefore, it appears to be one of the most fundamental variables that determine structure, abundance and biomass of marine benthic systems (Pearson and Rosenberg, 1978).

The lagged abundance responses of taxa to the nutrient concentration may be explained by the fact that most species that substantially contributed to abundance need two or more growing seasons after their recruitment to reach adult size and to appear in the macrozoobenthos fraction of our samples. Beukema et al. (2002); Josefson et al. (1993) and Frid et al. (1996) observed similar time lags of a few years in the marine benthos as a response to increased nutrient concentrations.

Among the environmental variables we studied in the DFA model, only salinity was not clearly related to the temporal variability of benthic macrofaunal abundance. Surface salinity varied largely during the study period but had no noticeable effect on the long-term dynamics of the benthic macrofauna. This might be partly due to the fact that salinity variations are much lower in the benthic environment of the deeper waters studied here and to the ability of most benthic taxa to cope with variations in salinity (Neumann et al., 2008). However, we should not preclude indirect effects induced by planktonic processes, which are more directly influenced by surface water salinity fluctuations and which are beyond the scope of this study. Other factors, such as disturbance of the sediments by bottom fisheries, are other sources of variability in benthic communities (Callaway et al., 2002) and should be carefully considered in order to reduce unexplained variability, once appropriate data for these factors are available.

4.3. Contribution of specific taxa to the temporal variability

Canonical correlation and factor loading produced quite similar results that suggest a good match between MAFA and DFA models. Both techniques identified those taxa which correlated best with the overall temporal trend of the macrofauna. *Callianassa* spp., *S. filicornis*, *T. flexuosa*, *Spisula* spp. were related to both MAFA axes and the common trend of the DFA. These species are relatively small, short-lived, fast-growing deposit feeders and their abundance was related to the MAFA axis and the common trend. This close relationship to the MAFA axis and the common trend may reflect that populations consisting of such "opportunistic" small, short-lived, fast-growing species respond quickly and strongly (in terms of change in abundance) to environmental change (Dorsey, 1982).

Following the Pearson–Rosenberg model, it is possible to recognize the features of disturbed or stressed benthic communities. They are characterized by small organisms, high reproductive rates and high abundances of few species and are thus capable to proliferate as a result of ecological impact of various stressors (Como et al., 2007; Dorsey, 1982; Pearson and Rosenberg, 1978). They also show high turnover and biological productivity (as shown by higher values of production to biomass ratios, P/B).

In an unlikely case, when a community approaches the normal equilibrium state, one would assume that the biomass becomes dominated by a few species characterized by low abundance but large individual size and weight. In fact, opportunists are inherently poor competitors and may thus be out-competed by transition species and k-strategists if conditions improve.
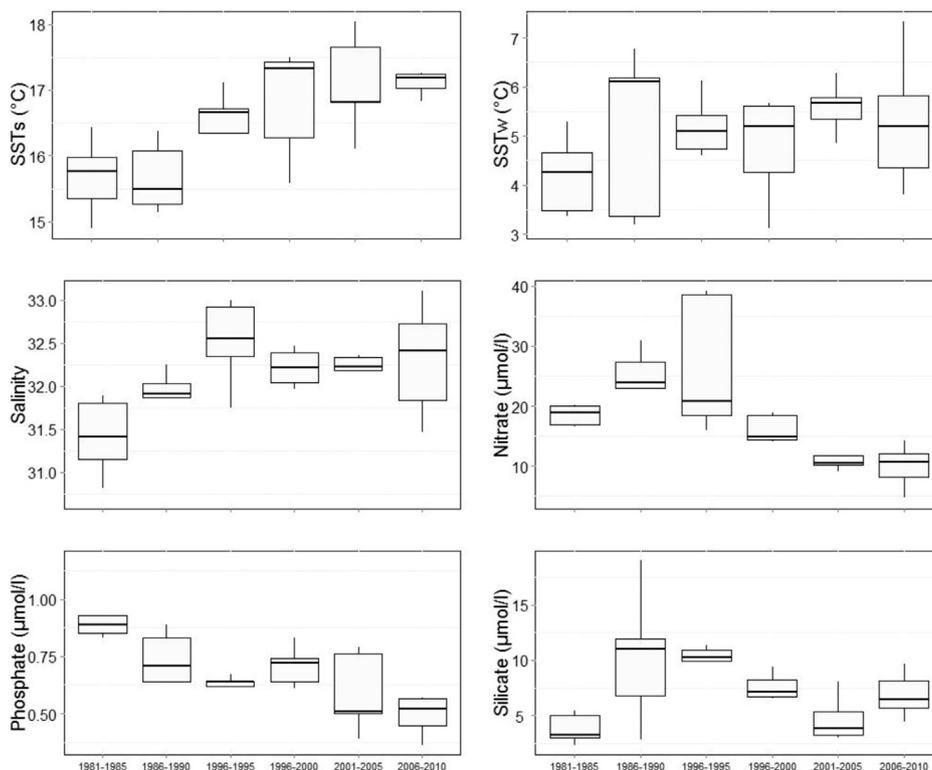
5. Conclusion

Our analysis indicates that temperature is the major abiotic determinant of macrobenthic temporal variability in the German Bight. This foresees that continuous future warming of North Sea waters, as predicted by different studies (e.g. Wiltshire et al., 2010) will affect the benthic macrofauna of the German Bight distinctly, with yet unpredictable consequences for benthic secondary production and associated ecosystem goods and services. Our results further indicate the importance of climatic extreme events, such as exceptionally cold winters, for the dynamics of the benthic macrofauna. Climatic extreme events are predicted to become more frequent in future decades (IPCC, 2013) potentially increasing the temporal variability of the benthic system and, thus, complicating the prediction of future developments. Opportunistic species contributed substantially to the variability of the benthic infauna indicating the importance of this group of species for the overall response of the benthos to environmental changes. A century of intense bottom trawling has substantially modified the marine benthos of the North Sea (Reiss et al., 2009). Continuous mechanical disturbance of the seafloor has reduced populations of large, long-living species, which were replaced by small, opportunistic species. This shift made the North Sea benthos more opportunistic and thus reactive to environmental fluctuations. Exclusion of bottom trawling activities from large areas of future offshore wind farms might allow for a recovery of the benthic community and an increase in abundances of non-opportunistic species (Gill, 2005). Depending on habitat type and scale, frequency and magnitude of fishing activities, recovery of benthic habitats after fishery closure may take up to eight years (Kaiser et al., 2000) or even longer (Duineveld et al., 2007). However, given the important role of warming in the development of benthic communities in the German Bight and the complex synergistic effects, it is difficult to predict the path that recovery might take even if the trawling stress were removed (O'Neill, 1998). This development toward a new situation might stabilize the benthic system and make it less susceptible to environmental fluctuations.

Appendix A. Variations in environmental variables in the German Bight. Data are aggregated in 5-year intervals. Boxes represent the inter-quartile range (IQR), with the horizontal line indicating the median and whiskers extending to the minima and maxima

Figure: boxplots of environmental variables (SSTs (°C), SSTw (°C), Salinity, Nitrate (μmol/l), Phosphate (μmol/l), Silicate (μmol/l)) across 5-year intervals: 1981–1985, 1986–1990, 1996–1995, 1996–2000, 2001–2005, 2006–2010.

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